Title

Plant trait covariance and nonlinear averaging: A reply to Koussoroplis et al.

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Publication Date

2019

DOI

10.3897/rethinkingecology.4.32767

Peer reviewed

Variance-Explicit Ecology: A Call for Holistic Study of the Consequences of Variability at Multiple Scales

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Variability or heterogeneity is everywhere in ecology and evolution. For instance, Levins (1968) introduces his classic work “Evolution in Changing Environments: Some Theoretical Explorations” as “a series of explorations … around the common theme of the consequences of environmental heterogeneity.” We have many reasons for studying variability at different levels, including within-individual variation through time or in modular organisms (e.g., tree branches); among or across individual variation in genetics or traits (including behaviors) within a population, guild, community, or ecosystem; or as environmental (e.g., meteorological, hydrological, limnological, oceanographic) drivers of processes of interest. Yet, ecologists most frequently manipulate the mean value of a driving variable of interest and look at its ecological effects and ignore variation in that driving variable or process of interest. For instance, we might rear an insect or plant at three average temperatures and then use analysis of variance to compare individual growth rates at these temperatures but overlook variation in temperature through time and its effects on growth rate{Note that “variations” as a plural does not work with “its” later in the sentence. We prefer keeping the focus on overall variation rather than individual variations}. Most frequently, patterns of spatial or temporal variation in either biotic or abiotic factors are used to make inferences about underlying mechanisms (e.g., using geostatistical techniques, Rossi et al. 1992 or using power law plots, Taylor 1961). Variation may even be treated as an

annoyance, requiring larger sample sizes to achieve statistical power or as unexplained variation for things that are stochastic or where mechanisms are not understood. As we aim to illustrate, although we have frameworks and sometimes good knowledge about direct effects of single forms of variation, we frequently miss important questions and opportunities about the mechanisms involved, how multiple forms and scales of variation combine, and effects across organizational levels.

A major unsolved problem in ecology is resolving the relative importance between different types and scales of variability to ecological processes. Organisms experience and respond to variation at many different biological and ecological levels, ranging from physiological to behavioral to populations and communities, and eventually to metapopulations, metacommunities, and geographic ranges. We will argue that certain forms of variation have been quite well studied, but that we lack research programs that might provide information about the relative importance of different mechanisms and interactions among them. Investigating these gaps might provide a mechanistic framework for how to understand how different forms of variation combine to affect ecological problems. A variety of general questions follow from our line of reasoning. What is the relative importance of different mechanisms by which variability influences ecology and what is the relative importance of variability at different scales? At what scales is variability averaged over so that it does not matter? At what scales does variability most influence ecology and how does it do so?

There have been several calls for more explicit consideration of the consequences of variability in ecology, either limited to particular mechanisms by which variation acts (e.g., through nonlinear averaging, Ruel and Ayres 1999), or effects on particular levels of ecological organization (e.g., Bolnick et al. 2011). There are a growing number of studies that do just that,

but most are restricted to one scale and type of variability. Moreover, most studies either focus solely on one mechanism or ignore mechanisms altogether and instead just measure the net effect of variation. An example of a kind of problem that ecologists have worked extensively on and for which we have a relatively good understanding of the role of variation is the literature linking plant diversity with plant yield (biomass production). Most of this literature indicates that increasing functional trait diversity (variability) in plant communities leads to increased plant biomass and greater overall resource utilization (e.g., Cardinale et al. 2006). This positive effect on biomass comes partly from a sampling effect and more substantially through niche complementarity and/or positive interspecific interactions (van Ruijven and Berendse 2005). Moving beyond plants, there is less understanding of the effects of plant trait diversity on higher trophic levels (e.g., Ruel and Ayres 1999, Benedetti-Cecchi 2000). A recent meta-analysis that we took part in suggests there could be relatively consistent negative effects of (within-species) variation in plant nutritional quality traits on average herbivore performance through the Jensen inequality {Please restore to the original. “Jensen’s Inequality” is the common name in the ecological literature and we would prefer to keep this recognizable form.}(Wetzel et al. 2016). Considering predators and herbivores, Mason et al. (2014) suggested that some generalist herbivores perform better feeding on a diversity of resources and that this may affect higher trophic levels; Arctiid caterpillars (*Grammia incorrupta*) were well defended against predators when they sequestered secondary metabolites from several different plant species but poorly defended when they sequestered compounds from only one plant species. Overall, such studies show that for certain problems we understand some mechanisms by which a particular form of variation acts on processes of interest. Equally well, the effects of certain forms of individual variation in altering population dynamics have been widely studied (e.g., Grimm 1999), as have

several other problems relating variation to processes within a single species or trophic level in ecology and evolution. There has been less work exploring how variation among multiple trophic levels combines to affect herbivore performance. For instance, how does variation in herbivore traits relate to variation in plant traits to affect herbivore performance (Moreira et al. 2016)?

To describe the background and elements required to proceed towards an integration of scales and types of variation and mechanisms by which variation acts, we present the following: (1) An overview of scales and types of biotic and abiotic variation by describing three frameworks for classifying them. (2) A summary of common mechanisms by which variation influences ecological dynamics. (3) A description of what might be gained by integrating different types and scales of variation. (4) We conclude by highlighting some next steps that could move us towards a conceptual framework for how organisms integrate multiple types and scales of variation.

Ways of classifying scales and types of variation

The literature describes a range of ways of classifying variation or that can be borrowed from classifications of other ecological patterns. We present three such classifications, one based on the structure of environmental variation, a second recognizing the hierarchical nature of biological or ecological organization, and a general scheme that might be applied to any type of variation.

Environmental Variation

Environmental variation is most commonly viewed as the physical, chemical, and geological factors that are largely independent of biotic factors at least over the time scales of most concern to ecologists; such factors were termed “scenopoetic” in an ecological niche context by Soberón and Arroyo-Peña (2017). Such environmental variation merits separate consideration from biotic

variation because it has its own scaling and structure, occurring continuously from microscopic to global scales. For example, temperature varies temporally at a scale of minutes as clouds pass in front of the sun, at a scale of hours as the sun rises, peaks, and sets; at a scale of months as the seasons progress; at scales of years to decades (sunspot cycles, el Niño {confirming that the suggested edit is good}cycles etc.); and at geologic timescales through glacial cycles. Environmental variation may have stochastic and predictable components. Some work also separates recurrent stochastic components from extreme events, including hurricanes, floods, and fires (e.g., Shaffer 1981, Yang et al. 2008, Yang et al. 2010). Temporal environmental variation is often somewhat cyclical and predictable, as exemplified by daily temperature cycles, seasonal variation, and sunspot cycles. Spatial variation often increases with distance. For instance, Bell et al. (1993) studied variation in physical variables in lakes or soil nutrients from a variety of geographic areas and found that, in general, environmental variation continued to increase with spatial scale of study (distance). The scaling of different environmental factors with distance or with time has been used to identify relevant processes in studies of scaling (Levin 1992, Storch et al. 2007). Denny (2015) describes how to use principles from engineering and physics to understand both physical environment interactions and subsequent species interactions through what he terms “ecological mechanics.”

The extent to which environmental (and biotic) variation is encountered by an organism depends on its scale of movement, longevity, and life cycle. Within life cycles, periods of dormancy versus intense resource use are particularly relevant. Spatial and temporal variation are both potentially relevant in several ways. McPeek and Kalisz (1998) modeled the effect of spatial, temporal, and spatiotemporal variation on the evolution of dormancy versus dispersal, finding that pure temporal variation promotes dormancy and that spatial and spatiotemporal

variation promote dispersal. Cyclical seasonal migration of North American and European passerine birds is known to be a response to extreme temperatures (Newton and Dale 1996a,b), whereas Australian butterflies respond to extreme dry conditions (Dingle et al. 2001).

In some cases, biotic factors may interact with abiotic factors, and even then, it may be a valid simplification to separately consider abiotic environmental factors if we are studying processes that operate at very different timescales relative to the rate of change of environmental factors through biotic–abiotic coupling (e.g., many ecosystem processes). However, if we were studying long-term tree growth, then a feedback between habitat fragmentation and microclimate might be relevant (e.g., Laurance and Williamson 2001); for long-lived perennial grasses mineral nutrients in soils may depend on grazing history (e.g., McNaughton et al. 1997). For such processes it would make sense to instead think about how to combine different forms of biotic and abiotic variation into analyses.

Biotic Variation

Biotic variation in traits relevant to ecological interactions occurs from subindividual to between individuals within a species or across species. Raw genetic and somatic variation within individuals (or part of them), expressed as traits including behaviors that vary in timing and sequence, may relate to subspecific (e.g., races, morphs) variation, other taxonomic levels, and to higher organizational levels within ecology, paleobiology, biogeography, and other biological sciences. A brief tour of relevant levels of biotic organization helps to identify some of the things that each level contributes or emphasizes. Of course, lower-level variation is included in higher organizational levels but may or may not have effects on higher-level processes. For instance, there is a growing literature on community and ecosystem genetics that investigates the effects of genotype on processes from communities to ecosystems (Whitham et al. 2003).

At the level of within-individual variation, individual organisms frequently respond in plastic ways to ambient environmental and biotic conditions, including behaviors, physiological acclimation, developmental flexibility, life-historical changes in timing, and as ecological engineers (Jones et al. 1997). Critically, such plasticity changes both variability encountered and the relationship between this variability and emergent or higher-level processes performed by the organism. Although there is a great deal of literature on behavioral plasticity, developmental plasticity, life histories, and related subjects, it is unusual for studies to make links to emergent higher-level processes of interest. Beyond plasticity, individual history may produce changes in organisms. A plant phenotype might vary through time depending on the history of herbivory and plant responses to herbivory through inducible defenses (Adler and Karban 1994, Karban and Baldwin 1997). Individual history of infection may alter the susceptibility to the same or new diseases in the future in ways that are either positive or negative. Carryover effects from one habitat to another may produce a relevance of spatial history (e.g., Talley et al. 2006), and there are several named temporal carryover effects (e.g., maternal effects) that produce time-lagged responses (e.g., Ratikainen et al. 2008). Organisms with repeating structures, such as plants with multiple leaves and reproductive organs, may produce especially high variation among organs within individuals (Herrera 2009).

Variability among individuals within a population is recognized as intraspecific trait variation (e.g., Bolnick et al. 2011), arising through phenotypic plasticity, genetic diversity (Hughes et al. 2008), and ontogeny, including life histories and history more generally. Just as species may have different population dynamics, or serve different roles in communities or ecosystems, the same is true of individuals with different traits within a species. Intraspecific variation has been a recent focus of study in ecology (e.g., reviews by Hughes et al. 2008,

Bolnick et al. 2011), yet as far back as the 1970s Lomnicki (1978) pointed out that population regulation could not occur if all individuals within a population were identical. Recent synthetic analyses indicate that approximately 30% to 50% of the total variation in plant functional traits in plant communities occurs at the intraspecific level, with intraspecific variation being especially large for chemical traits and smaller for physical traits (Albert et al. 2010, Messier et al. 2010, Siefert et al. 2015).

A population is not necessarily the appropriate scale at which to study variation. At a higher level, sections or subpopulations within a population may sometimes be identified, or analogously populations with a metapopulation. They are described using variables such as phenotype frequencies, population densities (e.g. aggregations, congregations), or sex ratios within populations. Population cohorts may be identifiable based on time of birth, leading to a temporal structure, and such temporal variation is known to produce cyclical population dynamics (e.g. Kendall et al. 1999). Alaska sockeye salmon provide a good example of population segments, with stream- versus lake-spawning individuals varying in morphology (e.g. Blair et al. 1993).

Another form of variation is created by species diversity, making guilds, communities, and ecosystems relevant. Ecologists are familiar in population, community, and ecosystem ecology with studying the effects of species diversity or interspecific differences (both forms of variability) on processes of interest. Interspecific variation may have effects through direct or indirect species interactions within a guild, or more diffuse community or ecosystem-level effects. Species richness, multivariate dispersion of communities (e.g., principal components analysis (PCA) of species' abundances), functional diversity, phylogenetic diversity, and variation in interaction strength within a food web all capture elements of across species

variation. Such variation may also be the complex outcome of the action of biological and environmental factors, and emergent effects of such variation, which is the sum of what we describe in this chapter. At some level, diversity begets diversity, in that the variation experienced by an organism may be a response to variation within a community. Hence there may be a rapid scaling up of the potential for complex effects of species diversity on organisms, just as the potential for higher-order species interactions increases rapidly with the number of species in a community.

Pattern and Structure of Variation

Irrespective of whether variation is biotic or abiotic we can consider whether variation is essentially unstructured within the scope of the process under exploration, or whether there is a pattern or structure involved. In a more specific form of this, Adler et al. (2001) pointed out that spatial heterogeneity is composed of spatial variance and spatial pattern (structure). Although spatial variance is necessary for spatial heterogeneity, spatial variation may or may not be organized into a spatial pattern. Unstructured snapshots may be typical of a foraging herbivore if plants of different quality are essentially randomly distributed within the area within which it can forage and during the relevant time period. On the other hand, Tobler's first law of geography reminds us that near things tend to be more similar than far things, which lends structure and predictability to spatial variance (Tobler 1970). Such spatial autocorrelation typically has characteristic spatial scales. For example, a species of herbivorous beetle tended to occur in clumps of its host plant of 25–50 m in diameter and separated from neighboring clumps by 200–300 m (Talley 2007). Temporal variation reflects daily, lunar, solar, and longer-term processes such as El Niño, Pacific Decadal Oscillation, and sunspot and glacial cycles, but also the less-predictable components of weather and seemingly random and often extreme events. Temporal

autocorrelation and the unidirectionality of history structure such variation.

Some Existing Mechanisms by Which Variation Influences Ecological Processes

Mechanisms by which variation alters a process of interest include general mechanisms that can apply to any ecological level of organization and some that are specific to particular organizational levels. Consequently, it is a large topic and we aim to be illustrative rather than encyclopedic in our descriptions but encourage readers to think beyond the mechanisms we include. We first describe some more general mechanisms and then describe those that relate more closely to biology and ecology.

General Mechanisms: Mathematical Functions as Filters, and Effects of Nonlinearity of Functions

Considering mathematical functions (e.g., $y = f(x)$) as filters provides a broad view of their role in changing variation between the input (x) and output (y) variables (Denny and Benedetti-Cecchi 2012). Trait variation interacts with responses to biotic and abiotic variation to determine the inputs to filters. The outputs are the ecological processes of interest and either the average outputs or variation in outputs may be of interest. Such a filtering view is frequently expressed in the literature about scaling in ecology, asking if variation at one level is present at another (e.g., Storch et al. 2007). Peter Chesson's scale-transition theory provides a mathematical framework for formally analyzing systems of equations to investigate such changes (Chesson 2012). Feedback processes, such as density and frequency dependence, can either amplify or cancel out variation from the input to the output. More generally, different forms of variation may act additively, synergistically, or antagonistically. Ideas about resonance emphasize that processes acting at different temporal or spatial frequencies may amplify or cancel out variation (e.g.,

Blarer and Doebeli 1999). Such ideas are interesting and poorly explored given that both individual growth and population growth have associated timescales, and that density-dependent functions produce characteristic return times for populations returning to an equilibrium (e.g., Luckinbill and Fenton 1978). Nonlinear equations have the ability to amplify variation, as is emphasized in the literature on chaotic dynamics (e.g., Hastings et al. 1993); viz., small amounts of variation in initial conditions can lead to large differences in the emergent (population) dynamics. The approach led Hastings et al. (1993) to ask questions about nonlinear dynamics, such as what are the respective roles of endogenous and exogenous factors, and do they interact? More generally, determining the role of variation in an input variable on a process of interest requires us to determine if the dynamics are nonlinear or not.

Another important effect of nonlinearity of functions is how variation in an input variable affects the average value of the output variable, our process of interest. Jensen's inequality describes the role of nonlinearity in altering the output from a mathematical function (reviewed by Ruel and Ayres 1999). Variation in an input variable to a function that is concave down will reduce the average value that is given by the function relative to a linear function, and a convex function does the opposite. Sibly et al. (2005) found that most population time series produced nonlinear and concave curves for per-capita growth as a function of population size (or density); consequently, variation in population density reduces average population size below the equilibrium abundance (carrying capacity). (The statistics of Sibly et al. were criticized in several published comments but the general point about the shape of functions and effect of variation is well illustrated by the example.) Nonlinear or nonmonotonic functions are common in ecology and arise through a variety of mechanisms, as reviewed by Zhang et al. (2015). Mechanisms leading to nonlinearity include the law of tolerance, whereby species underperform

with either too little or too much of a required ecological factor (Shelford 1931), through the action of adaptive behaviors or physiological adaptation altering relationships between environmental factors and organismal responses, or by sequentially combining multiple synergistic (or antagonistic) factors so as to produce nonlinear outcomes (Zhang et al. 2015). The strong role of nonlinearity leads us to question whether we should be using general mechanistic functional forms for particular problems (e.g., functional responses of predators to prey, or allometric equations), or whether we should use more flexible functional forms to represent arbitrary forms of nonlinearity (e.g., cubic splines (Schluter 1988), or response surface methodologies (Inouye 2005)){I'm not sure how you want to format the last parenthetical examples with their citations: perhaps there is a better style to avoid parentheses within parentheses. We prefer to keep this as one long sentence if we can but to shorten it to make it less unwieldy}. Nonmechanistic statistical equations can still be used to infer things like the size of a Jensen effect or whether environmental variation as an input is amplified or damped down in the output from the mathematical function of interest. In some cases, nonlinear averaging may serve as a null model to predict the expected effect (Koussoroplis et al. 2017). For instance, Pearse et al. (2018) looked at how experimental variance in the concentration of a plant toxin in artificial diet {'artificial diet' is a thing}altered herbivore performance and found that nonlinear averaging predicted toxin variance would enhance performance, whereas the observed effect was negative. The authors hypothesized that the costs of physiological acclimation in the face of trait variance (Wetzel and Thaler 2016) explained the difference between the predicted and observed results.

Mechanisms Involving Biology and Ecology

Physiological Responses and Consequences

When individuals directly encounter biotic or abiotic variability within their lifetime and are unable to use behavioral mechanisms to avoid it, it is likely to have important physiological consequences. Variability is especially important for organismal physiology because when it is high it encompasses extreme values, which is when physiological stress is expected to be greatest and the consequences of not dealing with conditions may be most harmful. This occurs because relationships between environmental variables and organismal performance tend to be concave-down over large environmental ranges as expressed by Shelford's law of tolerance (1932); the general mechanism behind this is Jensen's inequality (or nonlinear averaging), discussed previously.

The physiological responses of consumers to diet species diversity—trait diversity at the guild or community level—are especially well studied. It was long believed that diverse diets helped consumers achieve balanced nutrient intake and diluted the effects of toxic defenses associated with any one prey species (Bernays et al. 1994). A recent meta-analysis, however, indicates that mixed-species diets tend to be no better for consumers than the best single-species diet, and they are typically worse than the best single-species diet when diet species possess chemical defenses (Lefcheck et al. 2013). This suggests that consumers facing greater diet variability may experience reduced physiological performance (Wetzel and Thaler 2018). It is often not clear how to view heterogeneity within diets. For instance, Marzetz et al. (2017) show that the chemical composition of algal species as food are more important to growth rates of *Daphnia* than are the algal species' identities or diversity. One general way forward may be to use colimitation theory to integrate several physical and/or biotic factors into a single unified conceptual framework that incorporates potential nonlinearities that arise in a multivariate context, but which are not apparent when factors are considered unidimensionally (Koussoroplis

et al. 2017).

Organisms can have important physiological adaptations that help them cope with variability. These take the form of physiological plasticity, which allows organisms to change their physiology to maximize performance under current conditions, or fixed phenotypes that are useful for coping with variable environments. Examples of plastic responses to variability include insect herbivores that reshape their digestive chemistry in response to changing plant conditions (e.g., Bolter and Jongsma 1995), and tadpoles, which change gut size in response to predation risk and food availability (Relyea and Auld 2004). If phenotypic alterations of this nature are costly, which they certainly are for insect herbivores acclimating to plant conditions, then high variability could lead to costly repeated acclimation (Wetzel and Thaler 2016). Rather than changing physiology to match current biotic and abiotic conditions, some organisms pay a permanent cost to be constantly ready for changing conditions. For example, 38 predatory fish species maintained gut sizes two- to three-fold larger than necessary for the average amount of prey they encountered; this allowed them to be ready to process rare pulses of high food abundance (Armstrong and Schindler 2011).

Behavioral Responses and Consequences

Movement, activity patterns and resource selection are major ways that organisms modulate the amount and type of abiotic and biotic variability that they experience. We often think about resource selection as having the goal of getting an organism to resources of a certain quality or quantity, but resource selection is likely to be vital for coping with variability in resource quality and quantity. Optimality theory suggests a wide range of ways organisms reduce costs, such as decisions when to leave patches in response to declining food quality (from the marginal value theorem) (MacArthur and Pianka 1966; Charnov 1976), or when to consume less-profitable food

items (from optimal diet theory) (e.g. Emlen 1966). Game theory shows how such decisions can be contingent on other individuals if an organism is maximizing resource intake (or some other currency). Similarly, habitat selection behavior modifies the environmental variation that an organism experiences (e.g., Morris 2003). These central ideas in behavioral ecology alter the relationship between variability encountered and a fitness-related output. Of course, for real organisms the ability of such behaviors to reduce variability between input and output has its limits. For instance, Sih and Christensen (2003) identified conditions such as prey mobility that prevented predators from foraging optimally, and which may therefore lead to a more direct relationship between prey variation and variation in food intake.

Extreme variation may also be coupled with unusual and interesting behaviors. Nomadism is thought to arise in response to extremes of spatiotemporal variation in resource availability or environmental conditions. For instance, desert locust outbreaks track spatiotemporally variable rainfall and subsequent periods of plant germination and growth (Jonzén et al. 2011). Environmental variation that is novel to an organism may also produce different ecological effects to that which is routinely encountered. Hence, Sih and colleagues coined the term human-induced rapid environmental change (HIREC) to draw attention to anthropogenic changes that place organisms under conditions (e.g., population) the species has not experienced before and may produce either individual- or population-level responses (Robertson et al. 2013).

Population and Community Responses and Consequences

Population and community responses to variation are numerous. Various mechanisms for the consequences of and responses to trait variation were reviewed by Bolnick et al. (2011) and serve as a starting point: (1) diversification of species interactions, such as increased generalism,

through traits affecting the kinds of interactions and with which other individuals or species focal individuals interact; (2) a portfolio effect produced by covariation among individuals with different traits; (3) phenotypic subsidy whereby genetic variation or plasticity decouple phenotype and fitness; (4) trait variation as a source of adaptive variation in rapid evolution; and (5) sampling effects whereby small populations contain only a small number of traits. Population ecologists often relate variation to extinction risk through population viability analyses and decompose mechanisms into those involving demographic and environmental stochasticity, or more extreme catastrophes (Shaffer 1981). At a multispecies level there is a large body of research on indirect interactions that are trait- or density-mediated (e.g. Bolker et al. 2003), indirect effects (e.g.,, Menge 1995), and positive versus negative species interactions (e.g., Tylianakis et al. 2008). All the above serve as potential mechanisms for how interspecific variation modifies processes of interest. Surprisingly little empirical work has evaluated the mechanisms described by Bolker et al. (2003) and their relative importance.

Metapopulation and Metacommunity Responses and Consequences

Source–sink dynamics (Pulliam 1988) and habitat-specific demography recognize that habitat areas have heterogeneous effects on population dynamics. Similarly, species sorting and mass effects ideas from metacommunity theory do the same for whole communities (Leibold et al. 2004). Rescue and mass effects across space alter the ability of species to cope with low-quality habitats (Pulliam 1988; Leibold et al. 2004). Most frequently, such ideas are applied to constant habitat heterogeneity, but we can also view habitats as changing, as captured by ideas about source–sink inversions (e.g., Boughton 1999) or temporally autocorrelated environmental conditions (Gonzalez and Holt 2002). Local adaptation may drive whether populations are sources or sinks and modify source–sink dynamics (e.g. Dias 1999), or metacommunity

dynamics (Urban et al. 2008).

The Motivation for Integrating Different Forms of Variation and Processes of Interest

As outlined in the Introduction, although the effects of variation in some processes have been quite well studied, three related problems have been poorly explored: (1) consideration of multiple forms of variation, (2) consideration of variation at multiple scales, and (3) the relative importance of different mechanisms by which variation influences ecology. Nor are interactions among types of variability usually a subject of study. Consider a focal herbivore species feeding on a single species of plant and which is fed on by a specialist predator. This scenario includes variation in the physical environment and that which arises from variation within, and emergence of, variation across three interacting species or trophic levels. Variation in the physical environment might (for example) include spatial variation in mineral nutrients, water availability, and climatic variation at multiple space and time scales that can act on any species. A natural question is what forms of physical variation affect each species? To what extent does plasticity of any kind reduce the relationship between variation in a physical variable and processes of interest in each species? Or conversely do some forms of physical variation actually lead to increased variation in the process of interest? Does individual variation produce different outcomes of the process of interest, and is the net effect to dampen or enhance variation in the process of interest? The answers to such questions mean that we should also be interested in what the biological and ecological mechanisms are, and what kinds of mathematical functions can be used to represent them. Species interactions could also dampen (filter) or amplify variation in traits of one species in their population dynamics or other processes in which the species participates. Again the ecological and biological mechanisms and functional forms are of

interest.

Individuals experience variance in abiotic and biotic conditions within their lifetime, and simultaneously the population encompassing those individuals experiences interindividual variability, and again simultaneously populations within a metapopulation experience landscape-level variability. It is well established that variability on one scale matters for adjacent scales. An unresolved question is if variability matters for more distant scales. For example, we know fine-scale abiotic variability matters for individual physiology, but how does it influence population or metapopulation dynamics? This question harks back to Levin's (1992) MacArthur Award{it is the MacArthur Award of the Ecological Society of American and is not a MacArthur Fellowship} lecture, in which he argues, "The key to understanding how information is transmitted across scales is to determine what information is preserved and what information is lost as one moves from one scale to the other." In the quarter-century since Levin pointed out this gap in our understanding, surprisingly little empirical work has been done on the topic.

For the species involved, their encounter with variation and responses to it will depend on their movements, activity periods, and degree of selection of resources (or physical conditions). Although we frequently study foraging, we rarely view it from a variation perspective to understand how foraging behaviors affect quality and quantity of resources acquired relative to variability in these things. The pattern (structure) and scale of resources are relevant (as well as resource-specific aspects of depletability and substitutability). Other questions are: Does the species adjust its foraging movements in relation to resource quality? What is the net effect of any resource selection behavior? Does selection (and other plasticity) reduce variation in individual growth or survival of the consumer? How is the population growth rate of the consumer species affected? There may also be feedbacks such that resource quality or quantity is

affected by previous species interactions, and spatiotemporal patterns of variation in resources may alter competition among individual consumers. The consumer interacts with its predator through a variety of top-down and bottom-up forces. Are there detectable signals from predators of variation in the physical environment that affect plant quality and subsequently herbivores? If it is a top-down process, how do predators integrate spatiotemporal variation into processes of interest?

Questions also arise at more general levels. For instance, thinking about tritrophic interactions in general we might ask about the importance of different mechanisms in producing variation in a response variable of interest. Further, are there characteristic nonlinear shapes of processes (functions) of interest? How does the scale of movement of different kinds of species relate to variation in resource quality in the environment?

Conclusion: What Are the Next Steps in Moving towards an Understanding of How Multiple Scales and Types of Variation Interact to Influence Ecological Processes?

As stated above, a major unsolved problem in ecology is resolving the relative importance of different types and scales of variance, and the relative importance of the different mechanisms by which variance can influence ecological dynamics. With the exception of variation through species composition or trait variation (e.g., biodiversity and ecosystem functioning studies), studies that actually manipulate variation to look at the effects on ecological dynamics are rare (e.g., Underwood 2004, 2009, Pearse et al. 2018). And studies that do manipulate variation tend to manipulate genetic diversity but ignore the traits and mechanisms underlying the ecological effects of variability (Crutsinger 2015). We need more studies that examine and manipulate

variance at multiple scales and compare the consequences; for instance, studies that manipulate trait diversity at both intra- and interspecific scales (Cook-Patton et al. 2011). Model species such as crop plants in which species have been bred to exhibit particular traits may be a good starting point for the often-difficult job of creating trait variation under carefully controlled conditions. However, investigating many forms of variation require us simply to recognize and quantify existing patterns and use them in new manipulations of variation. We also need more studies that experimentally isolate different mechanisms by which variance influences ecology (section 3). Does variation at certain scales have typical mechanisms of action or types of consequences? Under what circumstances are different types of mechanisms (e.g., Jensen's inequality versus effects via phenotypic plasticity) more important?

Making progress in answering these questions is likely to involve collaborations among different types of biologists, from physiologists to behavioral ecologists to community and ecosystem ecologists. We already possess a formidable array of mathematical tools for investigating the effects of variation. Certain forms of environmental variation have been the targets of research in population ecology, such as reddening spectra to produce autocorrelated temporal variation (Gonzalez and Holt 2002), or the effects of timescales of variation in producing resonance through interaction with intrinsic population dynamics (Orland 2003). There is no reason why we cannot look at the effects of multiple scales of environmental variation on ecological dynamics. In such investigations, like any investigations of variation, careful parameterization of mathematical functional forms and analysis of any nonlinearities can show whether there is an effect on the average or variance of the output variable. Collaborations between mathematical ecologists and empiricists are likely to be especially fruitful. Ultimately, we need to move towards research programs aimed at investigating the role of variation in

ecological dynamics.

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